

Catalog of the Fossil Isoptera of the New World

by

Luiz Roberto Fontes¹ & Maria Aparecida Vulcano²

ABSTRACT

A Catalog on the New World fossil termites, termite ichnofossils and related subjects is presented. The number of taxa registered are: 22 genera (of which 10 are exclusively fossil) and 34 species, 4 ichnogenera and 4 ichnospecies.

INTRODUCTION

The interest on fossil termites and termite traces enlarged considerably in the last decade. A series of new scientific acquisitions and concepts has contributed to this. As examples, we mention the exploration of new deposits of the Cretaceous age (mainly the Santana Formation in the northeast region of Brazil), descriptions of many ichnofossils (including nests and tunnels), studies on the essential role of termites in the metamorphosis of tropical soils and rocks (including soil formation and regeneration, and the major contribution of the insect to laterite formation), and new technology on molecular biology that has put termites in evidence through studies of DNA of fossil specimens.

Recent accounts, with discussion and a comprehensive bibliography, are available on the fossil history of termites (Thorne *et al.* 2000), insect trace fossils (Genise *et al.* 2000), ancient patterns of termite nest construction (Genise & Bown 1994), and termites of the Santana Formation and the contribution of termites to the genesis of laterites (Fontes & Vulcano 1998).

The New World has now 22 genera, of which 10 are exclusively fossil, and 34 species of fossil termites. There is also a considerable collection of information on termite traces (including the description of 4 ichnogenera and 4 ichnospecies) and other related subjects, as symbiotic and parasitic organisms, and data on molecular biology of fossil species.

LIST OF ABBREVIATIONS FOR TYPE DEPOSITORIES

AMNH — American Museum of Natural History, New York, USA.

DNPM — Divisão de Paleontologia, Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil.

¹Caixa Postal 42043, CEP 04073-970 São Paulo, SP, BRAZIL. E-mail: lrfontes@uol.com.br and lrfontes@cupim.net. URL: <http://www.cupim.net>

²Rua dos Pessegueiros, 144, cep 05673-010 São Paulo, SP, BRAZIL

LACM — Los Angeles County Museum, Los Angeles, USA.

MACN — Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina.

MAVC — M. A. Vulcano, São Paulo, Brazil (private collection).

MCFLC — Museo de la Ciencia de la Fundación La Caixa, Barcelona, Spain.

MCZC — Museum of Comparative Zoology, Cambridge, USA.

MLPC — Museo de La Plata, Buenos Aires, Argentina.

MPUC — Museum of Paleontology, University of California, Berkeley, USA.

PEFO — Petrified Forest National Park Museum, Arizona, USA.

PUIC — Princeton University Collection of Paleontological Invertebrates, Princeton, USA.

USNM — National Museum of Natural History (previously United States National Museum), Washington, USA.

FOSSIL ISOPTERA

Bibliography: Burnham 1978: 85-93; Carpenter 1992; Fontes & Vulcano 1998; Thorne *et al.* 2000.

HODOTERMITIDAE

CARINATERMITINAE

CARINATERMITINAE Krishna & Grimaldi, 2000: 134-136.

Carinatermes Krishna & Grimaldi, 2000: 134.

Type species: *C. nascimbeni* Krishna & Grimaldi 2000.

C. nascimbeni Krishna & Grimaldi, 2000: 136-137, Figs. 1-2 (alate: head, pronotum, fore wing, fore coxae, posterior tip of abdomen, cercus, tibia and tarsus).

Type locality: USA, New Jersey, White Oaks (Crossman's) Pits, Sayreville. Turonian, Upper Cretaceous. Type: AMNH (nr. NJ-124).

Bibliography: Thorne *et al.* 2000, fig. 5b (alate).

CRETATERMITINAE

CRETATERMITINAE Emerson 1967: 278-281.

Cretatermes Emerson, 1967: 284-285.

Type species: *C. carpenteri* Emerson, 1967.

C. araripena (Krishna), 1990: 76-77, Figs. 1-3 (alate: head, pronotum, fore leg, cercus, fore and hind wings) [*Meiatermes*].

Type locality: Brazil, Chapada do Araripe. Santana Formation, Lower Cretaceous. Type: AMNH (nr. 43902).

Bibliography: Fontes & Vulcano 1998: 246-265, Figs. 1-28 (alates). see Fig. 1 (below) and Fig. 2 (overleaf).

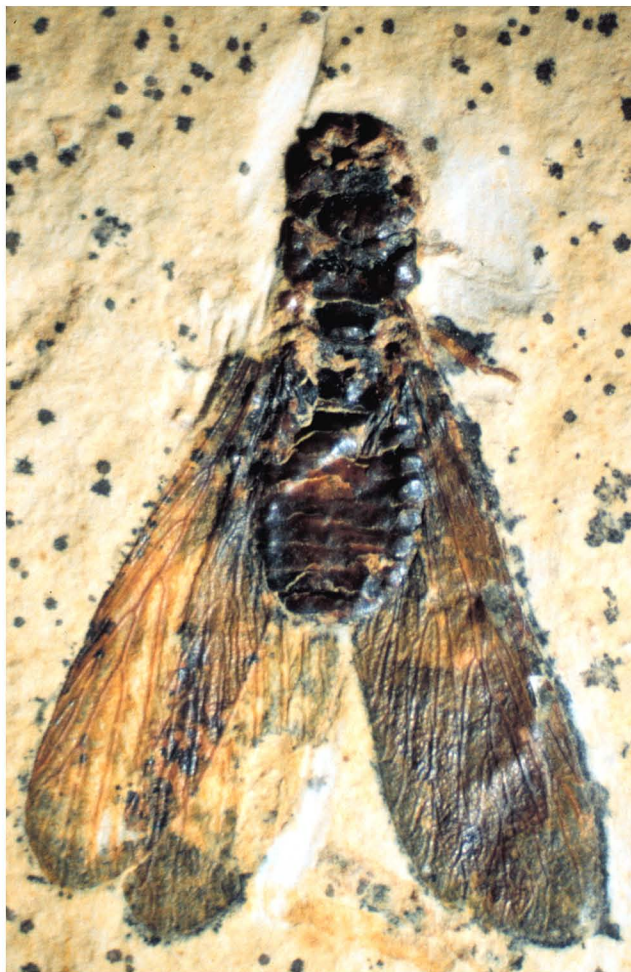


Fig. 1. *Cretatermes araripena*, alate in dorsal view. Body and wings reasonably preserved. Pronotum and part of head (with left eye) well preserved. Collection of MAVC (nr. 5002)

C. carpenteri

Emerson, 1967: 285-288, Figs. 1-3 (fore wing).

Type locality: Canada, Labrador: near Schefferville (54°50'N, 67°00'W).

Type: PUIC (nr. 87270).

Bibliography: Grassé 1986, Fig. 274 (fore wing); Thorne *et al.*, 2000, Fig. 5a (fore wing).

C. pereirai

Fontes & Vulcano, 1998: 265-269, figs. 29-30, 35-38 (alate).

Type locality: Brazil, Chapada do Araripe. Santana Formation, Lower Cretaceous. Type: MAVC (nr. 2452).



Fig.2. *Cretatermes araripena*, alate in dorsal view, Body reasonably preserved, with wings contour. Some appendices of the head and parts of the pronotum preserved. Collection of MAVC (nr. 1718)

HODOTERMITINAE

Mariconitermes Fontes & Vulcano, 1998: 269-270.

Type species: *M. talicei* Fontes & Vulcano, 1998.

M. talicei Fontes & Vulcano, 1998: 270-276, Figs. 31-34, 39-42 (alate: head, pronotum, mesonotum, metanotum, cerci).

Type locality: Brazil, Chapada do Araripe. Santana Formation, Lower Cretaceous. Type: MAVC (nr. 5006). Fig. 3 (at right)



Fig. 3. *Mariconitermes talicej*, dealate in dorsal view. Well preserved specimen. Holotype, collection of MAVC (nr. 5006)

Ulmeriella Meunier, 1920: 728.

Type species: *U. bauckhorni* Meunier 1920.

Bibliography: Emerson, 1968: 6-10 (revision).

U. latahensis

Snyder, 1949b: 164, Fig. 1 (hind wing).

Type locality: USA, Washington: Cut nr. 1, Portland Seattle Railroad (47°40'N, 117°25'W). Latah Formation, Upper Miocene. Type: USNM.

Bibliography: Emerson 1968: 18-19.

U. rubiensis Lewis, 1973: 1359-1360, Fig. 1 (wing).

Type locality: USA, Montana, Alder. Oligocene. Type: AMNH.

KALOTERMITIDAE

Bibliography: Krishna 1961; Emerson 1969.

Calcaritermes

Type species: *C. imminens*, (Snyder 1925) [*Kalotermites*] (extant).

C. vetus Emerson, 1969: 39-43, Fig. 10 (alate).

Type locality: Mexico, Chiapas, Vega de la Campam (São Pedro River, Simojovel

region). Amber, Oligocene-Miocene. Type: MPUC.

Distribution: Mexico, Ixhuatan (Tapilula River = Teapa River).

Cryptotermes

Type species: *C. cavifrons* Banks, 1906 (extant).

C. ryshkoffi Pierce, 1958: 19, pl. 5, Fig. 1 (wings), pl. 6, Fig. 6 (rock nodule).

Type locality: USA, California, Calico Mts. Type: LACM.

Bibliography: Emerson, 1969: 52-53.

C. yamini Krishna & Bacchus, 1987: 2-3, Figs. 1-2 (alate).

Type locality: Dominican Republic. Amber, Upper Oligocene or Lower Miocene. Type: AMNH.

Incisitermes

Type species: *I. schwarzi* (Banks, 1920) [*Kaloterme*s] (extant).

I. krishnai Emerson, 1969: 46-52, Fig. 12 (alate).

Type locality: México, Chiapas, Simojovel region. Amber, Miocene-Oligocene. Type: MPUC.

Synonym: *Kaloterme*s *nigritus* Snyder, 1960: 493 (not Snyder, 1946; wrong identification), México.

Proelectrotermes von Rosen, 1913: 331 [*Caloterme*s subg. *Proelectrotermes*].

Type species: *P. berendtii* Pictet, 1854 [*Termes*].

Bibliography: Emerson, 1942: 9, 10; Krishna, 1961: 317-318; Emerson, 1969: 14-15; Engel & Krishna, 2001.

P. fodinae (Scudder) 1883: 141 (alate) [*Paroterme*s].

Type locality: USA, Colorado, Florissant. Lower Oligocene (cf. Emerson, 1971: 282). Type: MCZC.

Bibliography: Emerson 1969: 19-22, Fig. 5 (A: mandibles, B: pronotum, C: wing).

Prokalotermes Emerson 1933: 189.

Type species: *Prokaloterme*s *hageni* Scudder, 1890.

Bibliography: Krishna 1961: 331; Emerson, 1969: 11-12.

P. (?) alderensis Lewis 1976: 313-315, Fig. 1 (alate).

Type locality: USA, Montana, Alder. Upper Oligocene. Type: AMNH.

P. hageni (Scudder) 1890: 110, 112, pl. 12, Fig. 2 (alate) [*Paroterme*s].

Type locality: USA, Colorado, Florissant. Lower Oligocene (cf. Emerson, 1971: 282). Type: MCZC.

Bibliography: Emerson 1969: 12-14, fig. 3 (A: mandible; E: wing).

MASTOTERMITIDAE

Bibliography: Emerson 1965.

Blattotermes Riek, 1952: 17-20.

Type species: *B. neoxenus* Riek, 1952.

Bibliography: Emerson 1965: 24, Fig. 1 (distribution of species).

B. wheeleri (Collins), 1925: 406, Fig. 2 (fore wing) [*Mastotermes*].

Type locality: USA, Tennessee, Grand Junction (35°03'N, 89°10'W).

Lower Eocene. Type: USNM.

Bibliography: Emerson 1965: 25.

Mastotermes Froggatt, 1896: 517, 519.

Type species: *M. darwiniensis* Froggatt 1896 (extant).

Bibliography: Emerson 1965: 25-28, Figs. 2-3 (distribution of species).

Synonym: *Pliotermes* S. Pongrácz 1917: 28. Type species: *P. hungaricus* S. Pongrácz, 1917.

M. electrodominicus Krishna & Grimaldi, 1991: 3-6, Figs. 1-3 (nymph), 4-15 (alate).

Type locality: Dominican Republic. Amber, Upper Oligocene or Lower Miocene. Type: AMNH.

Bibliography: Thorne *et al.* 2000, fig. 6 (A: alate; B: worker; C: soldier).

M. electromexicus Krishna & Emerson, 1983: 2-7, Figs. 1-2 (alate), 3 (soldier), 4 (nymph).

Type locality: Mexico, Chiapas, Simojovel Region (18°19'N, 92°40'S). Amber, Upper Oligocene or Lower Miocene. Type: MPUC.

Spargotermes Emerson, 1965: 19-21.

Type species: *S. costalimai* Emerson, 1965.

S. costalimai Emerson, 1965: 21-24, Figs. 1 (distribution), 4a-c (wing).

Type locality: Brazil, Minas Gerais, Distrito de Alvinópolis, Fonseca (20°10'S, 43°18'W). Type: DNPM.

Bibliography: Grassé 1986, Fig. 247 (hind wing).

Synonym: *Mastotermes*? sp. Lima 1944: 291-292, plate (wing).

TERMOPSIDAE

Bibliography: Engel *et al.* 2003.

TERMOPSINAE

Bibliography: Emerson 1933.

Parotermes Scudder, 1883: 135-137.

Type species: *P. insignis* Scudder 1883.

Bibliography: Emerson 1933: 171-172.

P. insignis Scudder, 1883: 137-139 (alate).

Type locality: USA, Colorado, Florissant. Lower Oligocene (cf. Emerson, 1971: 282). Type: MCZC.

Bibliography: Zittel 1885: 773, Fig. 974 (wing); Scudder, 1890: 108, pl. 12, Figs. 13-14; Emerson, 1933: 168 (key), 172, Figs. 5-7 (left mandible, pronotum, tarsum).

Zootermopsis

Type species: *Z. angusticollis* (Hagen 1858) [*Termopsis*] (extant).

Z. (?) coloradensis (Scudder), 1883: 142-143 (alate) [*Hodotermes*].

Type locality: USA, Colorado, Florissant. Lower Oligocene (cf. Emerson, 1971: 282). Type: MCZC.

Bibliography: Scudder 1890: 113, pl. 12, Fig. 6; Cockerell 1908, Fig. without number (p. 118; alate) [*Hodotermes*]; Emerson 1933: 187-188, Fig. 40 (fore wing).

Synonym: *Parotermes scudderi* Cockerell, 1913: 8. Type locality: USA, Colorado, Florissant. Lower Oligocene. Bibliography: Snyder, 1925: 154, 159 (notes).

RHINOTERMITIDAE

Bibliography: Emerson 1971; Krishna & Grimaldi, 2003.

COPTOTERMITINAE**Coptotermes**

Type species: *C. gestroi* (Wasmann, 1896) [*Termes*] (extant).

C. priscus Emerson, 1971: 268-270, Fig. 3a,d (alate: pronotum, wing).

Type locality: Dominican Republic. Amber, Oligocene-Miocene. Type: AMNH.

C. sucineus Emerson, 1971: 270-272, Fig. 3b-c,e (alate: pronotum, wing).

Type locality: Mexico, Chiapas, B-5103 (ca. 23 km SE Simojovel). Amber, Upper Oligocene or Middle Miocene. Type: MPUC (nr. 12679B).

Bibliography: Snyder 1960, plate 70, Fig. 1 (alate on left side).

HETEROTERMITINAE

Heterotermes

Type species: *H. platycephalus*, Froggatt 1925 (extant).

H. primaevus Snyder, 1960: 493-494, pl. 70, Figs. 1 (alate on right side)-2 (alate).

Type locality: Mexico, Chiapas, B-5103 (ca. 23 km SE Simojovel). Amber, Upper Oligocene or Middle Miocene. Type: MPUC (nr. 12679A).

Bibliography: Emerson 1971: 274-276, Fig. 5a-d (alate).

Reticulitermes

Type species: *R. flavipes* (Kollar 1837) [*Termes*] (extant).

R. creedei Snyder, 1938: 109, pl. 13, Fig. 3 (wing).

Type locality: USA, Colorado, near Creede. Type: MCZC.

Bibliography: Emerson, 1971: 284-285.

R. fossarum (Scudder), 1883: 143 (alate) [*Eutermes*]

Type locality: USA, Colorado, Florissant. Lower Oligocene. Type: MCZC (Lectotype nr. 271).

Bibliography: Emerson 1971: 281-282. Scudder 1890: 115, pl. 12, Fig. 20 (alate)

Synonym: *Eutermes meadti* Scudder, 1883: 144-145. Type locality: USA, Colorado, Florissant. Lower Oligocene. Type: MCZC (Lectotype nr. 272). Bibliography: Scudder, 1890: 115, pl. 12, Figs. 12, 17 (alate).

R. laurae Pierce, 1958: 20-21, pl. 5, Fig. 3 (wing), pl. 6, Fig. 8 (rock nodule), pl. 7, Fig. 10 (wing).

Type locality: USA, California, Calico Mountains. Lower Miocene. Type: LACM.

Bibliography: Emerson 1971: 285-286, Figs. 8-9 (wings).

RHINOTERMITINAE

Dolichorhinotermes

Type species: *D. longilabius* (Emerson, 1925) [*Rhinotermes*] (extant).

D. dominicanus Schlemmermeyer & Canello, 2000: 305, Figs. 1-3 (alate).

Type locality: Dominican Republic. Amber, Miocene. Type: MCFLC (nr. MCFLC/MCAM-0248).

STYLOTERMITINAE

Bibliography: Emerson 1971: 287.

Parastylotermes Snyder & Emerson (*in* Snyder), 1949: 366, 378.

Type species: *Stylotermes washingtonensis* Snyder 1931.

Bibliography: Emerson 1971: 290-292.

P. calico Pierce, 1958: 20-21, pl. 5, Fig. 2 (wing), pl. 6, Fig 7 (rock nodule).

Type locality: USA, California, Switchback Canyon, Yermo Quadrangle (ca. 35°00'N, 116°51'W), Calico Mountains (San Bernardino County). Middle Miocene. Type: LACM.

Bibliography: Emerson 1971: 295, Fig. 15 (wing).

P. frazieri Snyder, 1955: 80, Fig. 1 (wing).

Type locality: USA, California, Ventura County (Old Frazier Borax Mine), Mt. Pinos Quadrangle. Middle Miocene. Type: USNM.

Bibliography: Emerson, 1971: 294-295.

P. washingtonensis (Snyder), 1931: 317, pl. 1, Fig. 5 (wing) [*Stylotermes*].

Type locality: USA, Washington, near Spokane. Upper Miocene. Type: MCZC.

Bibliography: Snyder, 1948: 16, Fig. 4 (wing); Emerson, 1971: 295-296 (wing).

TERMITIDAE

TERMITINAE

Gnathamitermes

Type species: *G. perplexus* (Banks, 1920) [*Amitermes*] (extant).

G. rousei Pierce, 1958: 21-22, pl. 5, Fig. 5 (wing), pl. 6, Fig. 9 (rock nodule) [*Gnathamitermes magnoculus rousei*].

Type locality: USA, California, Calico Mountains. Miocene. Type: LACM.

Bibliography: Krishna, 1996: 2, taxonomy (*G. magnoculus rousi* and *G. rousi*, wrong spelling).

NASUTITERMITINAE

Bibliography: Fontes 1998 (worker digestive tube; phylogeny of Neotropical genera).

Constrictotermes

Type species: *C. cyphergaster* (Silvestri, 1901) [*Eutermes*] (extant).

Bibliography: Krishna, 1996: 3-7.

C. electroconstrictus Krishna, 1996: 3-4, Figs. 1-2 (head of soldier), Fig 3 (soldier).

Type locality: Dominican Republic. Amber, Upper Oligocene or Lower Miocene. Type: AMNH.

Nasutitermes

Type species: *N. sanchezi* (Holmgren, 1910) [*Eutermes*] (extant). This name is a junior synonym of *N. costalis* (Holmgren, 1910), as designated by Emerson (1925: 379), but valid as type species according to the International Code of Zoological Nomenclature (Sands 1965: 15-17).

Bibliography: Krishna 1996: 4-8.

N. electrinus Krishna, 1996: 10-11 (alado).

Type locality: Mexico, Chiapas, Simojovel region (18°19'N, 92°40'W). Amber, Upper Oligocene or Lower Miocene. Type: MPUC.

N. electronasutus Krishna, 1996: 8-10, Figs. 7-8 (head of soldier).

Type locality: Dominican Republic. Amber, Upper Oligocene or Lower Miocene. Type: AMNH.

Unidentified

Schlee & Gloeckner 1978, coverpicture.

Locality: Dominican Republic. Amber, Upper Oligocene or Lower Miocene.

Bibliography: Schlee 1980, pl. 35 (head of soldier); Boucot 1990: 479, Figs. 389 (entire soldier), 390 (head of soldier).

Unidentified

Muellermeister 2001: 15 (Fig. of worker), 21 (Fig. of three soldiers).

Locality: Dominican Republic. Amber, Upper Oligocene or Lower Miocene.

TERMITE ICHNOFOSSILS

Nest and fecal pellets within wood

Bibliography: Boucot, 1990: 376-378, 482; Genise, 1993a.

KALOTERMITIDAE***Incisitermes******I. cf. minor***

Lance, 1946: 21-27, Fig. 1 (tar-impregnated root of *Pinus* with fecal pellets), 2 (fecal pellets) [*Kaloterмес*].

Locality: USA, California, Santa Barbara County, Carpinteria. Pleistocene.

Bibliography: Boucot, 1990: 376.

Unidentified

Cycalichnus Genise, 1995: 294. Type species: *Cycalichnus garciorum* Genise 1995.

Cycalichnus garciorum Genise, 1995: 294-295, Figs. 1 (map), 2 (D: nest made of galleries with fecal pellets in a permineralized cycad stem; E: mass of fecal pellets), 5 (nest).

Type locality: Argentina, Rio Negro Province, 100 km N Valcheta. Upper Cretaceous. Type: MACN (nr. 53818).

Unidentified

Light 1930: 75-76, pl. 8, Figs. 1-2 (separated fossil fecal pellets and mass of fecal pellets), pl. 9 (magnified mass of fecal pellets, mineralized by calcium carbonate). In size the fossil pellets are similar to those of the extant species *Incisitermes schwarzi* [*Kaloterмес*], also found in the same region (p. 76; pl. 8, Fig. 3, fecal pellets).

Locality: USA, Florida, St. Petersburg. Pleistocene.

Unidentified

Rogers 1938: 389-392, Figs. 1 (chambers and galleries in conifer wood packed with fecal pellets), 2-3 (thin section of opalized fecal pellets). No identification of family or genus originally assigned.

Locality: USA, California, Santa Barbara County, Santa Maria. Pliocene.

Unidentified

Rohr *et al.*, 1986: 87-88, Figs. 2 (galleries and frass), 3 (silicified fecal pellets).

Locality: USA, Texas, Brewster County. Upper Cretaceous. USNM (nr. 349402).

Bibliography: Boucot 1990: 377-378, fig. 310 (fecal pellets).

TERMOPSIDAE

Zootermopsis

Z. cf. nevadensis

Lance 1946: 21-27, Figs. 1 (tar-impregnated root of *Pinus* with fecal pellets), 3 (fecal pellets).

Locality: USA, California, Santa Barbara County, Carpinteria. Pleistocene.

Bibliography: Boucot 1990: 376.

TRACE GALLERIES AND TERMITIC REMAINS IN THE MANTLEROCK

General bibliography: Machado 1983b; Grassé 1986.

Fontes, 1984a-b (lateritic subsoil in the Amazon Region: Tucuruí, Pará State, Brazil).

Fontes & Vulcano 1998: 285-291 (tunnels in lateritic subsoil in the Amazon Region: Tucuruí, Pará State, Brazil; Figs. 43-44: block of subsoil of residual basaltic origin crossed by termitic small and large galleries).

Hasiotis & Dubiel 1995: 121-125 (galleries and chambers of *Archeoentomichnus metapolypholeos*; Fig. 5: subterranean galleries and chambers).

Machado 1983a (termitic remains in bauxite from Guatemala); 1987 (pisolithic ferruginous bauxite from Canada is not of Precambrian age, but Cretaceous or Tertiary; Fig. 1: map; Figs. 2-6: rock and structural details; Figs. 7-23: animal and plant remains; Fig. 24: termite gut protozoan); 1994 (role of termite gut protozoans in the fixation of iron oxides in laterites; universal occurrence of gut microfossils in laterites; gut microfossil composition of silt fraction of soil is similar to those of laterites; Fig. 7: microfossils from silt of soil from Tucuruí, State of Amazonas, Brazil).

Martins & Leonardos 1992 (pelletal structures with sulfides in laterites; Fig. 1: termite bioturbation in the excavation site; Figs. 2-6: pellets).

Taltasse 1957 ("Cabeças de Jacaré" Formation, Floriano, Piauí State, Brazil; Fig. 1: map; Figs. 2-3: tunnels in soil profile; Fig. 2 reproduced in Grassé, 1986: 435, Fig. 244).

SUBTERRANEAN NESTS AND GALLERIES

Bibliography: Boucot 1990: 473- 475, 482; Genise 1993b: 54.

Cornitermes

Tacuruichnus Genise, 1997: 140. Type species: *Tacuruichnus farinai* Genise, 1997.

Tacuruichnus farinai Genise, 1997: 140-142, Figs. 1 (map), 2 (nest).

Type locality: Argentina, Buenos Aires Province, Miramar. Upper Pliocene. Type: phototypes (Fig. 2a of original paper).

Procornitermes

Locality: Argentina, Buenos Aires Province, General Pueyrredón. Upper Pliocene.

Bibliography: Laza 1995: 343-345, Fig. 1 (map).

Syntermes

Syntermesichnus Bown & Laza, 1990: 74. Type species: *Syntermesichnus fontanae* Bown & Laza, 1990.

Syntermesichnus fontanae Bown & Laza, 1990: 74-75, Figs. 1 (map), 2-4 (nest).

Type locality: Argentina, Santa Cruz Province, Arroyo Feo (46°57'01"S, 70°40'17"W). Miocene. Type: MLPC (nr. 24167).

Termes

Locality: Argentina, Buenos Aires Province, Necochea. Upper Pliocene to Lower Pleistocene.

Bibliography: Laza 1995: 345-347, Fig. 2 (map).

Unidentified

Archeoentomichnus Hasiotis & Dubiel, 1995: 121. Type species: *Archeoentomichnus metapolypholeos* Hasiotis & Dubiel, 1995.

Archeoentomichnus metapolypholeos Hasiotis & Dubiel, 1995: 121-125, Figs. 3-4 (nests), 5 (subterranean galleries and chambers).

Type locality: USA, Arizona, Petrified Forest National Park (34°54'45"N, 109°44'40"W). Upper Triassic. Type: PEFO (nr. 10348).

Unidentified

Hasiotis & Demko 1996: 364-365, Fig. 8 (subterranean galleries and nests closely associated to plant root systems or rhizoliths). No identification of family or genus originally assigned.

Locality: USA, Colorado and Utah States. Upper Jurassic.

Unidentified

Genise *et al.* 1998: 12-13 (nest similar to *Krausichnus* of Tertiary from Egypt or extant *Procornitermes* from South America).

Locality: Uruguay, Soriano Province, Pedro Chico (70 km NE Nueva Palmira). Upper Cretaceous to Lower Tertiary.

Unidentified

DeCelles & Horton 2003: 64 (nest similar to *Krausichnus* of Tertiary from Egypt), Figs. 6B-C.

Locality: Bolivia (Eastern Cordillera of southern central Bolivia). Oligocene to Early Miocene.

OTHER DATA RELATED TO FOSSIL TERMITES

Symbiotic microfossils

Machado 1987 (pisolithic ferruginous bauxite from Canada; fig. 24: termite gut protozoan); 1994 (role of termite gut protozoans in the fixation of iron oxides in laterites; universal occurrence of gut microfossils in laterites; gut microfossil composition of silt fraction of soil is similar to those of laterites; Fig. 7: microfossils from silt of soil from Tucuruí, State of Pará, Brazil).

Wier *et al.* 2002 (fossil symbiotic microbes in *Mastotermes electrodomenicus*, in amber from Costa Rica; Fig. 1: termite in amber; Figs. 2-4: fossil protists; Fig. 5: fossil plant tissue).

Parasitic fungi

Poinar & Thomas 1982 (mycelial growth of insect-parasitic fungi, probably *Entomophthora*, covering the abdomen and thorax of a termite worker from Dominican amber; Fig. 1: termite in amber with white mycelial growth; Fig. 2: mycelium and conidiophores).

Molecular biology (DNA)

DeSalle *et al.* 1992 (DNA was extracted from *Mastotermes electrodomenicus* preserved in Oligo-Miocene amber, and fragments of mitochondrial and nuclear genes were amplified); 1993 (PCR amplification of *M. electrodomenicus* DNA resulted in recombinant clones).

DeSalle *et al.*, 1993 (PCR jumping in clones of DNA extracted from *Mastotermes electrodomenicus* preserved in Oligo-Miocene amber).

REFERENCES

- Boucot, A.J. 1990. Evolutionary paleobiology of behavior and coevolution. Elsevier Science Publishers, 750 pp.
- Bown, T.M. & J.H. Laza 1990. A Miocene termite nest from southern Argentina and its paleoclimatological implications. *Ichnos* 1: 73-79.
- Burnham, L., 1978. Survey of social insects in the fossil record. *Psyche* 85: 85-133.
- Carpenter, F.M., 1992. Order Isoptera Brullé, 1832, pp. 137-142. *In*: Treatise on invertebrate paleontology. Vol. 3, The Geological Society of America & The University of Kansas.
- Cockerell, T.D.A., 1908. Florissant: a Miocene Pompeii. *Popular Science Monthly* 73: 112-126.
- Cockerell, T.D.A., 1913. The genera *Parotermes* and *Hodotermes* (Isoptera). *Entomological News* 24: 6-8.
- Collins, R.L., 1925. A lower Eocene termite from Tennessee. *Amer. J. Sci* (5)9: 406-410.
- DeCelles, P.G. & B.K. Horton 2003. Early to middle Tertiary foreland basin development and the history of Andean crustal shortening in Bolivia. *Geological Society of America Bulletin* 115(1): 58-77.
- DeSalle, R, M. Barcia & C. Wray 1993. PCR jumping in clones of 30-million-year-old DNA fragments from amber preserved termites (*Mastotermes electrodomenicus*). *Experientia* 49(10): 906-909.
- DeSalle, R,J. Gatesy, W. Wheeler & D. Grimaldi 1992. DNA sequences from a fossil termite in Oligo-Miocene amber and their phylogenetic implications. *Science* 257(5078): 1933-1936.
- Emerson, A.E. 1925. The termites of Kartabo, Bartica District, British Guyana. *Zoologica* 6(4): 291-459.
- Emerson, A.E. 1933. A revision of the genera of fossil and recent Termopsinae (Isoptera). *Univ. Calif. Publ. Entom.* 6(6): 165-196.
- Emerson, A.E. 1942. The relations of a relict South African termite (Isoptera, Hodotermitidae, *Stolotermes*). *American Museum Novitates*, nr. 1187, 12 pp.
- Emerson, A.E. 1965. A review of the Mastotermitidae (Isoptera) including a new genus from Brazil. *American Museum Novitates*, nr. 2236: 1-64.
- Emerson, A.E. 1967. Cretaceous insects from Labrador. 3. A new genus and species of termite (Isoptera: Hodotermitidae). *Psyche* 74(4): 276-289.
- Emerson, A.E. 1968. A revision of the fossil genus *Ulmeriella* (Isoptera, Hodotermitidae, Hodotermitinae). *American Museum Novitates*, nr. 2332, 22 pp.
- Emerson, A.E. 1969. A revision of the Tertiary fossil species of the Kalotermitidae (Isoptera). *American Museum Novitates*, nr. 2359, 57 pp.
- Emerson, A. E. 1971. Tertiary fossil species of the Rhinotermitidae (Isoptera), phylogeny of genera and reciprocal phylogeny of associated flagellate (Protozoa) and the Staphylinidae Coleoptera. *Bulletin of the American Museum of Natural History* 146(3): 243-304.

- Engel, M.S. & K. Krishna 2001. Case 3164: *Kaloterme*s Hagen, 1853 (Insecta, Isoptera): proposed designation of *Termes flavicollis* Fabricius, 1793 as the type species. Bulletin of Zoological Nomenclature 58(2): 100-104. [approved in ICZN, 2002. Opinion 2007. *Kaloterme*s Hagen, 1853 (Insecta, Isoptera): *Termes flavicollis* Fabricius, 1793 designated as the type species. Bulletin of Zoological Nomenclature 59(3): 209-210]
- Engel, M.S., K. Krishna & C. Boyko 2003. Case 3244: Termopsidae Holmgren, 1911, *Termopsis* Heer, 1849 and *Miotermes* Rosen, 1913 (Insecta, Isoptera): proposed conservation of prevailing usage by the designation of *Termopsis bremiti* Heer, 1849 as the type species of *Termopsis*. Bulletin of Zoological Nomenclature 60(2): 119-123.
- Fontes, L.R. 1884a. Sub-recent activity of termites in the soil of the Amazon Region. Abstract, pp. 130-131, XI Congresso Brasileiro de Zoologia, Belém-PA.
- Fontes, L.R. 1884b. Sinais fósseis da ação de cupins. Ciência Hoje, Rio de Janeiro, 2(12): 52-54, 56.
- Fontes, L.R. & M.A. Vulcano 1998. Cupins fósseis do Novo Mundo, pp. 243-295. In: Fontes, L.R. & E. Berti Filho (Eds.), Cupins. O desafio do conhecimento. FEALQ, Piracicaba, Brazil, 512 pp.
- Fontes, L.R. 1998. Novos aditamentos ao "Catálogo dos Isoptera do Novo Mundo", e uma filogenia para os gêneros neotropicais de Nasutitermitinae, pp. 309-412. In: Fontes, L.R. & E. Berti Filho (Eds.), Cupins. O desafio do conhecimento. FEALQ, Piracicaba, Brazil, 512 pp.
- Genise, J.F. 1993a. Trazas fosiles de insectos en petrificaciones vegetales, pp. 41-47. In: Melchor, R.N. (Ed.), Nuevas tendencias en el estudio de trazas fosiles. Facultad de Ciencias Exactas y Naturales (UNLPam), La Pampa, Argentina.
- Genise, J.F. 1993b. Trazas fosiles de insectos en paleosuelos, pp. 49-59. In: Melchor, R.N. (Ed.), Nuevas tendencias en el estudio de trazas fosiles. Facultad de Ciencias Exactas y Naturales (UNLPam), La Pampa, Argentina.
- Genise, J.F. 1997. A fossil termite nest from the Marplatense stage (late Pliocene) of Argentina: paleoclimatic indicator. Palaeogeography, Palaeoclimatology, Palaeoecology 136: 139-144.
- Genise, J.F. & T.M. Bown 1994. New trace fossils of termites (Insecta: Isoptera) from the late Eocene - early Miocene of Egypt, and the reconstruction of ancient isopteran social behavior. Ichnos 3: 155-183.
- Genise, J.F., M.G. Mángano, L.A. Buatois, J.H. Laza & M. Verde 2000. Insect trace fossil associations in paleosols: the *Coprinitisphaera* ichnofacies. Palaios 15: 49-64.
- Genise, J.F., P.J. Pazos, M.G. Gonzáles, R.O. Tófolo & M. Verde 1998. Hallazgo de termiteros y tubos meniscados en la Formación Asencio (Cretácico Superior - Terciario Inferior) R. O. del Uruguay. Abstract, pp. 12-13, Tercera Reunión Argentina de Icnología y Primer Reunión de Icnología del Mercosur, Argentina.
- Grassé, P.-P. 1986. Termitières fossiles et latéritisation, pp. 428-438, 442-445. Sous-famille des Cretatermitinae, p. 501-503. In: Termitologia. Anatomie - physiologie - biologie - systématique des termites. Vol. 3, Masson, Paris, 715 pp.

- Hasiotis, S.T. & T.M. Demko 1996. Terrestrial and freshwater trace fossils, Upper Jurassic Morrison Formation, Colorado Plateau, pp. 355-370. *In*: Morales, M. (Ed.), The continental Jurassic. Museum of Northern Arizona Bulletin 60.
- Hasiotis, S.T. & R.F. Dubiel 1995. Termite (Insecta: Isoptera) nest ichnofossils from the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona. *Ichnos* 4: 119-130.
- Krishna, K. 1961. A generic revision and phylogenetic study of the family Kalotermitidae. *Bulletin of the American Museum of Natural History* 122: 303-408.
- Krishna, K. 1990. Isoptera. *Bulletin of the American Museum of Natural History* 195: 76-81.
- Krishna, K. 1996. New fossil species of termites of the subfamily Nasutitermitinae from Dominican and Mexican (Isoptera, Termitidae). *American Museum Novitates*, nr. 3176: 1-13.
- Krishna, K. & S. Bacchus 1987. A new fossil species of termite from Dominican amber, *Cryptotermes yamini* (Isoptera, Kalotermitidae). *American Museum Novitates*, nr. 2884: 1-5.
- Krishna, K. & A.E. Emerson, 1983. A new fossil species of termite from Mexican amber, *Mastotermes electromexicus*. (Isoptera, Mastotermitidae). *American Museum Novitates*, nr. 2767: 1-8.
- Krishna, K. & D. Grimaldi 1991. A new fossil species from Dominican amber of the living Australian termite genus *Mastotermes* (Isoptera: Mastotermitidae). *American Museum Novitates*, nr. 3021: 1-10.
- Krishna, K. & D. Grimaldi 2000. A new subfamily, genus, and species of termite (Isoptera) from New Jersey Cretaceous amber, pp. 133-140. *In*: Grimaldi, D. (ed.), *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden, 498 pp.
- Krishna, K. & D. Grimaldi 2003. The first Cretaceous Rhinotermitidae (Isoptera): a new species, genus, and subfamily in Burmese amber. *American Museum Novitates*, nr. 3390: 1-10.
- Lacasa-Ruiz, A. & X. Martínez-Delclòs 1986. *Meiatermes*: nuevo género fósil de insecto isóptero (Hodotermitidae) de las calizas Neocomienses del Montsec (Provincia de Lérida, España). *Institut d'Estudis Ilerdencs, Lleida, Spain*, 65 pp.
- Lance, J.F., 1946. Fossil Arthropods of California. 9. Evidence of termites in the Pleistocene asphalt of Carpinteria, California. *Bulletin of the Southern California Academy of Sciences* 45(1): 21-27.
- Laza, J.H., 1995. Signos de actividad de insectos, pp. 341-361. *In*: Alberdi, M. T., G. Leone & E.P. Tonni (Eds.), *Evolution biológica y climática de la región pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo Occidental*. Monografías del Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, Spain.
- Lewis, S.E. 1973. A new species of fossil Isoptera (Hodotermitidae) from the Ruby River basin (Oligocene) of Southwestern Montana. *Ann. Entomol. Soc. Amer.* 66(6): 1359-1360.
- Lewis, S.E. 1976. A new species of fossil Isoptera (Kalotermitidae) from the

- Ruby River basin (Oligocene) of Southwestern Montana. *Proc. Entomol. Soc. Wash.* 79(3): 313-316.
- Light, S.F. 1930. Fossil termite pellets from the Seminole Pleistocene. *University of California Publications in Geological Sciences* 19: 75-81.
- Lima, A.M.C. 1944. Sobre dois fósseis da bacia de Fonseca (Alvinópolis, Minas Gerais). *An. Acad. Brasil. Cienc.* 16(4): 291-292.
- Machado, A.B. 1983a. Termitic remains in some bauxites, pp. 251-254. *In*: Melfi, A.J. & A. Carvalho (Eds.), *Lateritisation processes. Proceedings, II International Seminar on Lateritisation Processes*, São Paulo, Brazil.
- Machado, A.B. 1983b. The contribution of termites to the formation of laterites, pp. 261-270. *In*: Melfi, A.J. & A. Carvalho (Eds.), *Lateritisation processes. Proceedings, II International Seminar on Lateritisation Processes*, São Paulo, Brazil.
- Machado, A.B. 1987. On the origin and age of the Steep Rock Buckshot, Ontario, Canada. *Chemical Geology* 60: 337-349.
- Machado, A.B. 1994. Massive presence of fossil termitic intestinal flagellates in laterites, pp. 35-38. *In*: Smith, B.J. & P.A. Warke (Eds.), *Eurolat 94, laterites, palaeoweathering and palaeosurfaces. Conference Proceedings*, Belfast.
- Martins, E.S. & O.H. Leonardos 1992. Estruturas peletais com sulfetos em lateritos resultantes de atividade de termitas. Abstract, pp. 577-579, 37º Congresso Brasileiro de Geologia, São Paulo, Brazil, *Boletim de Resumos Expandidos*.
- Meunier, F. 1920. Palaentology - Quelques insectes de l'Aquitaniien de Rott, Sept.-Monts (Prusse rhénane). *K. Akad. Wetensch. Amsterdam, Proc. Sect. Sci.*, 22(2): 727-737, 891-898, pl. 1, fig. 1.
- Muellenmeister, H.J. 2001. Bernstein-Poesie. Still-Leben aus grauer Vorzeit. Author's Edition, Germany, 48 pp.
- Pictet, F.J. 1854. *Traite elementaire de Paleontologie ou histoire naturelle des animaux fossiles*, 2nd ed., vol. 2 (termites: pp. 369-370). Separate Atlas, pl. 40, fig. 23.
- Pierce, W.D. 1958. Fossil arthropods of California. Nr. 21. Termites from the Calico Mountains nodules. *Bull. Southern Calif. Acad. Sci.* 57(1): 13-24, pls. 5-7.
- Poinar, G.O. & G.M. Thomas 1982. An entomophthoralean fungus from Dominican amber. *Mycologia* 74(2): 332-334.
- Riek, E.F. 1952. Fossil insects from the Tertiary sediments at Dinmore, Queensland. *Univ. Queensland Paper, Dept. Geol.*, 4(n.s.)(2): 15-22, 1 pl., 4 figs.
- Rogers, A.F. 1938. Fossil termite pellets in opalized wood from Santa Maria, California. *American Journal of Science*, ser. 5, 36: 389-392. Reprinted pp. 212-215 *In*: Sarjeant, W.A.S. (Ed.), 1983. *Terrestrial trace fossils*. Hutchinson Ross Publishing Company, Benchmark Papers in Geology nr. 76, 415 pp.
- Rohr, D.M., A.J. Boucot, J. Miller & M. Abbott 1986. Oldest termite nest from the Upper Cretaceous of west Texas. *Geology* 14: 87-88.
- Rosen, K. von 1913. Die Fossilen Termiten, ein kurz Zusammenfassung der bis jetzt bekannten Funde. *Trans. II Int. Congr. Entom.*, Oxford, Vol. 2: 318-

335, 6 pls.

- Sands, W.A., 1965. A revision of the termite subfamily Nasutitermitinae (Isoptera, Termitidae) from the Ethiopian region. Bulletin of the British Museum (Natural History), Entomology Supplement 4, 172 pp.
- Schlee, D. 1980. Bernstein-Raritäten. Staatl. Mus. Naturkd. Stuttgart, 88 pp.
- Schlee, D. & W. Gloeckner 1978. Bernstein. Stuttgarter Beiträe zur Naturkunde, Ser. C, vol. 8, 72 pp.
- Schlemmermeyer, T. & E.M. Canello 2000. New fossil termite species: *Dolichorhinotermes dominicanus* from Dominican amber (Isoptera, Rhinotermitidae, Rhinotermitinae). Papéis Avulsos de Zoologia, São Paulo, 41(20): 303-311.
- Scudder, S.H. 1883. The fossil white ants of Colorado. Proc. Amer. Acad. Arts and Sci., Boston, 19(n.s., 2)(1): 133-145.
- Scudder, S.H. 1890. The Tertiary insects of North America. U. S. Geol. Surv. Terr. 13: 102-116, pl. 12.
- Snyder, T.E. 1925. Notes on fossil termites with particular reference to Florissant, Colorado. Proc. Biol. Soc. Wash. 38: 149-166.
- Snyder, T.E. 1931. IV. Isoptera. In: Carpenter, F.M., Insects from the Miocene (Latah) of Washington. Ann. Ent. Soc. Amer. 24(2): 317, pl. 1, fig. 5.
- Snyder, T.E. 1938. Isoptera, fam. Rhinotermitidae, *Reticulitermes creedei*, n. sp. In: Carpenter, F.M. et al., Fossil insects from the Creede formation, Colorado. Psyche 45(2-3): 109-110, pl. 13, fig. 3.
- Snyder, T.E. 1946. A small, dark-colored new *Kalotermes* from Guatemala. Proc. Ent. Soc. Washington 48(6): 158-160.
- Snyder, T.E. 1948. Our enemy the termite. Comstock Publishing Co., New York, 257 pp.
- Snyder, T.E. 1949. Catalog of the termites (Isoptera) of the world. Smiths. Misc. Coll., Washington, 112: 1-490.
- Snyder, T.E. 1949b. A new Miocene *Ulmeriella* (fossil Isoptera, Hodotermitidae). Proc. Ent. Soc. Washington 51: 164-165.
- Snyder, T.E. 1955. A new fossil termite, *Parastylotermes frazieri*, from California (Isoptera, Rhinotermitidae). Proc. Ent. Soc. Wash. 57(2): 79-80.
- Snyder, T.E. 1960. Fossil termites from Tertiary amber of Chiapas, Mexico (Isoptera). J. Paleontol. 34(3): 493-494.
- Taltasse, P. 1957. Les "Cabeças de Jacaré" et le rôle des termites. Revue de Géomorphologie Dynamique 8: 166-170.
- Thorne, B., D. Grimaldi & K. Krishna 2000. Early fossil history of the termites, pp. 77-93. In: Abe, T., D.E. Bignell & M. Higashi (Eds.), Termites: evolution, sociality, symbiosis, ecology. Kluwer Academic Publishers, Dordrecht, The Netherlands, 466 pp.
- Wier, A., M. Dolan, D. Grimaldi, R. Guerrero, J. Wagensberg & L. Margulis 2002. Spirochete and protist symbionts of a termite (*Mastotermes electrodominicus*) in Miocene amber. Proc. Natl. Acad. Sci. 99: 1410-1413.
- Zittel, K.A. 1885. Handbuch der Paleontologie. Abt. 1, Band 2, p. 772-773.